

Separation of survival and movement rates in multi-state tag-return and capture-recapture models

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ABSTRACT *There has been growing interest in the estimation of transition probabilities among stages (Hestbeck et al., 1991; Brownie et al., 1993; Schwarz et al., 1993) in tag-return and capture-recapture models. This has been driven by the increasing interest in meta-population models in ecology and the need for parameter estimates to use in these models. These transition probabilities are composed of survival and movement rates, which can only be estimated separately when an additional assumption is made (Brownie et al., 1993). Brownie et al. (1993) assumed that movement occurs at the end of the interval between time i and $i + 1$. We generalize this work to allow different movement patterns in the interval for multiple tag-recovery and capture-recapture experiments. The time of movement is a random variable with a known distribution. The model formulations can be viewed as matrix extensions to the model formulations of single open population capture-recapture and tag-recovery experiments (Jolly, 1965; Seber, 1965; Brownie et al., 1985). We also present the results of a small simulation study for the tag-return model when movement time follows a beta distribution, and later another simulation study for the capture-recapture model when movement time follows a uniform distribution. The simulation studies use a modified program SURVIV (White, 1983). The Relative Standard Errors (RSEs) of estimates according to high and low movement rates are presented. We show there are strong correlations between movement and survival estimates in the case that the movement rate is high. We also show that estimators of movement rates to different areas and estimators of survival rates in different areas have substantial correlations.*

1 Introduction

Meta-populations are assemblages of local populations that are connected to each other by occasional migration and in which long-term persistence is determined

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by the processes of local colonization and extinction (Gilpin & Hanski, 1991). Meta-population theory is now a popular framework for understanding the threats faced by species in fragmented habitats. Theoretical, spatially realistic, mathematical models have been developed in order to make quantitative predictions about the dynamics of meta-populations.

Interpretation of spatially structured population systems is critically dependent on levels of migration between habitat patches (Harrison, 1994). All changes in numbers of individuals in a defined population result from changes due to birth, death, immigration, emigration, or a combination of these. Population ecologists have devoted disproportionate attention to studying and estimating birth and death rates and have only recently been integrating movements into explanations of how population numbers change over time (Hestbeck, 1995). It has been hard to make inferences concerning movement because there are limitations of data and methodology. Recent advances in methodology have allowed estimation of transition probabilities among states in the so-called multi-state capture-recapture models (Hestbeck *et al.*, 1991; Brownie *et al.*, 1993; Schwarz *et al.*, 1993).

These transition probabilities are composed of survival and movement rates. The separation of survival and movement rates is very important to conservation biologists interested in meta-populations and their management (Nichols *et al.*, 1992). In previous work, it was assumed that movement occurs at the end of the interval between time i and $i + 1$ (Nichols *et al.*, 1992; Brownie *et al.*, 1993). We generalize this work to allow different movement patterns in the interval for multi-state tag-recovery and capture-recapture experiments. The time of movement is modelled as a random variable with a known distribution. The model formulations in this paper are matrix extensions of the model formulations for single population tag-recovery and capture-recapture experiments (Jolly, 1965; Seber, 1965; Brownie *et al.*, 1985; Hoenig *et al.*, 1998a,b; Hearn *et al.*, 1998).

In the next section we develop the model. This is followed by the specific method for modelling movement time. We present a simulation study for the tag-return model and then another simulation study for the capture-recapture model. We conclude with a general discussion section that includes suggestions for future research including how to allow the time of movement distribution to be unknown.

2 Model definition

We use the Arnason-Schwarz model (Arnason, 1972, 1973; Schwarz *et al.*, 1993) to describe a multiple-state tag-recovery study. While our model is completely general, for simplicity we present a special case with $a = 2$ states, A and B , with $k = 3$ recovery occasions. The model extends the Brownie *et al.* (1985) models to multiple states. Matrix elements have superscripts that denote states and subscripts that denote time or tagging occasions.

The fundamental model parameters that can be estimated, given multiple years of recovery data, are defined (Brownie *et al.*, 1993; Hestbeck, 1995) as:

ϕ_i^s = the probability of being alive and in state s at time $i + 1$, for an animal alive and in state r at i (transition probability),
 p_i^r = the probability of capture at time i for an animal in state r at i (state capture probability).

$$\Phi_i = \begin{bmatrix} \phi_i^{AA} & \phi_i^{AB} \\ \phi_i^{BA} & \phi_i^{BB} \end{bmatrix}, \quad i = 1, 2 \text{ and } \mathbf{p}_i = \begin{bmatrix} p_i^A \\ p_i^B \end{bmatrix}, \quad i = 1, 2, 3$$

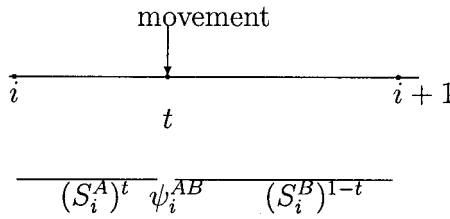


FIG. 1. Separation of survival and movement rates. For illustration, we display the survival and movement process for animals that begin in state A at time i and move to state B before time $i + 1$.

In addition, several parameters can be derived from the fundamental parameters. The derived parameters are defined as:

$(S_i^r)^t$ = the probability that an animal survives to time $i + t$, given that the animal was alive in state r at time i ,

ψ_i^{rs} = the probability that an individual is in state s at time $i + 1$, given that the animal survives to time $i + t$ and was in state r at time $i + t$,

$(S_i^s)^{(1-t)}$ = the probability that an animal survives to time $i + 1$, given that the animal was alive in state r at time $i + t$ and moved to state s at time $i + t$.

Transition probabilities are composed of survival and movement probabilities as shown in Fig. 1. For a fixed t we have:

$$\phi_i^{rs} = (S_i^r)^t \psi_i^{rs} (S_i^s)^{(1-t)}$$

For t from a known probability distribution $f(t)$, we have

$$\phi_i^{rs} = \int_0^1 (S_i^r)^t \psi_i^{rs} (S_i^s)^{(1-t)} f(t) dt \quad (1)$$

This is a new formulation. It is assumed that ψ_i^{rs} is constant, i.e. non-dependent on t ; and S_i^r and S_i^s are constant over the interval i to $i + 1$.

In addition, we assume that all individuals in state r at time i surviving from i to $i + 1$ must be located in a state, $s = 1, \dots, a$, at time $i + 1$;

$$\sum_{s=1}^a \psi_i^{rs} = 1$$

The statistics are defined as:

N_i^r = number of tagged animals released in state r at the beginning of the i th year,

R_{ij}^{rs} = number of animals with tags returned in state s at time j that were released in state r at time i ($i \leq j$).

$$\mathbf{N}_i = \begin{bmatrix} N_i^A \\ N_i^B \end{bmatrix}, \quad \mathbf{R}_{ij} = \begin{bmatrix} R_{ij}^{AA} & R_{ij}^{AB} \\ R_{ij}^{BA} & R_{ij}^{BB} \end{bmatrix} \text{ and } \mathbf{R}_{ii} = \begin{bmatrix} R_{ii}^{AA} \\ R_{ii}^{BB} \end{bmatrix}, \quad i(< j) = 1, 2, 3$$

Also, we define $D(\mathbf{p}_i)$ to be the diagonal matrix with diagonal elements equal to the elements p_i^r of the parameter vector \mathbf{p}_i (see Tables 1 and 2).

In capture-recapture studies, animals are released at a point in time and captured at a point in time, unlike tag-recovery experiments where recoveries take place over a period of time. In addition, an animal may be captured more than once in a

TABLE 1. Tag-return array

Year tagged	Number tagged	Year of recovery		
		1	2	3
1	N_1	R_{11}	R_{12}	R_{13}
2	N_2		R_{22}	R_{23}
3	N_3			R_{33}

TABLE 2. Multinomial cell probabilities of tag-return data

Year of tagged	Year of recovery		
	1	2	3
1	p_1	$\Phi_1 D(p_2)$	$\Phi_1 \Phi_2 D(p_3)$
2		p_2	$\Phi_2 D(p_3)$
3			p_3

TABLE 3. Capture-recapture array

Year tagged	Number tagged	Year of recovery		
		1	2	3
1	N_1	—	R_{12}	R_{13}
2	N_2		—	R_{23}
3	N_3			—

TABLE 4. Multinomial cell probabilities of capture-recapture data

Year of tagged	Year of recovery		
	1	2	3
1	—	$\Phi_1 D(p_2)$	$\Phi_1 D(1 - p_2) \Phi_2 D(p_3)$
2		—	$\Phi_2 D(p_3)$
3			—

capture-recapture study, but may be recovered only once in a tag-recovery study. Nevertheless, by a suitable redefinition of the parameters, and a slight change in data representation, similar methods may be used to estimate the parameters in capture-recapture studies (Schwarz *et al.*, 1993).

The expected number of recoveries in the capture-recapture formulation, in the case of three sample times, is displayed in Table 3. If we compare Table 3 with Table 1, we note that the diagonal elements of Table 3 are all zero, but the table has the same general form as Table 1. Table 4 is a reformulation of Table 2 using the tag-recovery notation.

Also, we define $D(1 - p_i)$ to be the diagonal matrix with diagonal elements equal to the elements $(1 - p_i)$ of the parameter vector.

The usual assumptions for tag-recovery models, as outlined by Brownie *et al.* (1985) and discussed by Nichols *et al.* (1982) and Pollock & Raveling (1982), are applicable. Also there are assumptions related to the multi-state structure of the

problem (Schwartz *et al.*, 1993). It is assumed that no animals migrate temporarily to a stratum where recoveries and releases do not occur, and do not return after one or more years of absence (animals may migrate out of the sampled strata permanently; such losses are indistinguishable from mortality); all animals behave independently with respect to migration and recovery (it is assumed that flocking or schooling of animals after release does not occur, or does not influence the migration pattern of the animal); animals behave in a Markovian fashion in each year, (i.e. the current migration route does not depend on previous migration choices); tag-reporting rates are available with estimates of their standard errors; the transition probability is the product of survival and movement rates in equation (1).

3 Modelling movement time

3.1 Known time of movement

Movement at the beginning or end of the interval ($t = 0$ or 1)

Previous work (Nichols *et al.*, 1992; Brownie *et al.*, 1993; Hestbeck, 1995) assumed that the movement time was known and was typically at the beginning or end of the interval ($t = 0$ or 1).

When movement occurs at the beginning of the interval between time i and $i + 1$, $\phi_i^{rs} = \psi_i^{rs} S_i^s$ for any states r and s . When movement occurs at the end of the interval between time i and $i + 1$, $\phi_i^{rs} = \psi_i^{rs} S_i^r$ for any states r and s .

Movement within the interval ($0 < t < 1$)

When movement occurs at a time other than 0 or 1, $\phi_i^{rs} = \psi_i^{rs} (S_i^r)^t (S_i^s)^{1-t}$ for any strata r and s . Explicit maximum likelihood estimates for survival and movement rates do not exist and have to be estimated iteratively.

3.2 Known distribution for the movement time

Here we wish to begin modelling movement in a more realistic way. We assume that movement occurs somewhere between the beginning and the end of the interval and that the time of movement has a known probability density function $f(t)$.

$$\phi_i^{rs} = \psi_i^{rs} \int_0^1 (S_i^r)^t (S_i^s)^{1-t} f(t) dt$$

Uniform distribution

When movement time is a random variable with the uniform distribution in the interval between time i and $i + 1$, $f(t) = 1$ so that

$$\begin{aligned} \phi_i^{rs} &= \psi_i^{rs} \int_0^1 (S_i^r)^t (S_i^s)^{1-t} dt \\ &= \psi_i^{rs} S_i^s \int_0^1 \left(\frac{S_i^r}{S_i^s} \right)^t dt \\ &= \begin{cases} \psi_i^{rs} S_i^s [\{ (S_i^r/S_i^s) - 1 \} / \{ \ln(S_i^r/S_i^s) \}] & \text{if } S_i^r \neq S_i^s \\ \psi_i^{rs} S_i^s & \text{if } S_i^r = S_i^s \end{cases} \end{aligned}$$

This is a very important case for biological reasons because it corresponds to the movement time being random in the interval. In addition, with this strong assumption, the distribution of movement time is completely determined, and no additional parameters have to be specified.

Beta distribution

When movement occurs as a random variable with the beta distribution in the interval between time i and $i + 1$,

$$\phi_i^{rs} = \psi_i^{rs} \int_0^1 (S_i^r)^t (S_i^s)^{1-t} f(t) \, dt$$

where $f(t)$ is the beta probability density function with parameters, α and β , such that α and β are known. (Of course, in practice, α and β would have to be obtained in some manner, i.e. perhaps estimated from a radio-telemetry study. We discuss this later.)

$$\begin{aligned} f(t) &= \frac{\Gamma(\alpha + \beta)}{\Gamma(\alpha)\Gamma(\beta)} t^{\alpha-1} (1-t)^{\beta-1} \\ \phi_i^{rs} &= \psi_i^{rs} S_i^s \int_0^1 \left(\frac{S_i^r}{S_i^s}\right)^t f(t) \, dt \\ &= \begin{cases} \psi_i^{rs} S_i^s \left(1 + \sum_{k=1}^{\infty} \left(\prod_{r=0}^{k-1} \frac{\alpha+r}{\alpha+\beta+r}\right) \frac{(\ln(S_i^r/S_i^s))^k}{k!}\right) & \text{if } S_i^r \neq S_i^s \\ \psi_i^{rs} S_i^s & \text{if } S_i^r = S_i^s \end{cases} \end{aligned}$$

We choose this case because the beta distribution is very flexible and allows symmetric and asymmetric movement distribution for t on the unit interval $(0, 1)$. We also note that if $\alpha = \beta = 1$, the beta distribution reduces to the uniform $(0, 1)$.

4 Numerical work on the tag-return model

We now present the results of a small simulation study for tag-recovery data carried out with a modified version of program SURVIV (White, 1983). We allowed the following factors to vary in 24 ($= 4 \times 2 \times 3$) cases, choosing values that we thought spanned a range of likely practical situations: (1) N , number tagged: we considered $N = 500$, $N = 1000$, $N = 2000$ or $N = 5000$ tagged in each period; (2) ψ , movement rate: we considered $\psi = 75\%$ (high) or $\psi = 25\%$ (low); (3) p , recovery rate: we kept p constant over patches and years, but assigned values 0.1, 0.2 or 0.4. We kept S (either S^A or S^B) constant each year, assuming reporting rate equals one effectively, but it could take the following values: when $p^A = p^B = 0.1$, $S^A = 0.8$, $S^B = 0.6$; when $p^A = p^B = 0.2$, $S^A = 0.7$, $S^B = 0.5$; when $p^A = p^B = 0.4$, $S^A = 0.6$, $S^B = 0.4$.

The beta distribution takes on many shapes, as the parameters α and β vary. We tried eight cases that give asymmetric ($\alpha > \beta$ or $\alpha < \beta$) and symmetric ($\alpha = \beta$) distributions with small and large variances. The case $\alpha = \beta$ yields a pdf symmetric about $\frac{1}{2}$ with mean $\frac{1}{2}$ (necessarily) and variance $(4(2\alpha + 1))^{-1}$. The pdf becomes more concentrated as α increases, but stays symmetric. If $\alpha = \beta = 1$, the beta

distribution reduces to the uniform (0, 1), showing that the uniform distribution can be considered to be a member of the beta family. The eight cases we considered were: ($\alpha = 4, \beta = 2$); ($\alpha = 8, \beta = 3$); ($\alpha = 1, \beta = 1$); ($\alpha = 2, \beta = 2$); ($\alpha = 5, \beta = 5$); ($\alpha = 8, \beta = 8$); ($\alpha = 2, \beta = 3$); ($\alpha = 5, \beta = 7$).

We carried out 500 simulations for each run. We calculated the relative bias of the estimates and the relative standard errors of the estimates. We define

$$\begin{aligned} \text{Relative bias } (\hat{\theta}) &= \text{Bias } (\hat{\theta})/\theta \\ \text{Relative SE}(\hat{\theta}) &= SE(\hat{\theta})/E(\hat{\theta}) \end{aligned}$$

where $\text{Bias}(\hat{\theta}) = E(\hat{\theta}) - (\theta)$; and $SE(\hat{\theta}) = \{E[\hat{\theta} - E(\hat{\theta})]^2\}^{1/2}$, the square root of the variance of the estimate.

In general, the converged number is smaller (Table 5), and relative bias and RSE being bigger (Tables 5-7) in the case of $\alpha < \beta$ with lower capture probability than in either $\alpha > \beta$ or $\alpha = \beta$ with higher capture probability, performing Monte Carlo simulations.

We found the bias to be very small ($< 2\%$ of the true parameters except having $< 5\%$ for \hat{S}^B where $N = 500, p^A = p^B = 0.1, S^A = 0.8, S^B = 0.6$) for the simulations where ψ was low. For the simulations where ψ was high, the bias was greatest for \hat{S}^B in either $\alpha > \beta$ or $\alpha = \beta$ ($< 9\%$ when $N = 500, < 6\%$ when $N = 1000, < 4\%$ when $N = 2000$, and $< 2\%$ when $N = 5000$), and it is much bigger ($< 13\%$ when $N = 500, < 10\%$ when $N = 1000, < 10\%$ when $N = 2000$, and $< 10\%$ when $N = 5000$) in $\alpha < \beta$. When S was held constant over the years (the reduced model), the bias was almost halved. The biases on \hat{S} and $\hat{\psi}$, where $\alpha < \beta$, were greater than those in the condition of either $\alpha > \beta$ or $\alpha = \beta$, the biases on \hat{S} being larger (Table 5).

We present the relative standard errors (RSEs, Appendix B.1-18 of Joe & Pollock, 2001) from all of our runs in low moving rate ($\psi = 0.25$) and high moving rate ($\psi = 0.75$). The RSEs are smaller when more animals are tagged. The RSEs are much smaller when p, ψ, S can be assumed to be constant over years, because then

TABLE 5. Converged numbers and Relative biases (%) of estimates of p, ψ, S where parameters vary over years or those are constant over years with high moving rate ($\psi = 0.75$), $p^A = p^B = 0.2, S^A = 0.7, S^B = 0.5, N = 1000$. There are three years of tag-recovery and two states

p, ψ, S	$\alpha = 4$	$\alpha = 8$	$\alpha = 1$	$\alpha = 2$	$\alpha = 5$	$\alpha = 8$	$\alpha = 2$	$\alpha = 5$
variable	$\beta = 2$	$\beta = 3$	$\beta = 1$	$\beta = 2$	$\beta = 5$	$\beta = 8$	$\beta = 3$	$\beta = 7$
	499	499	498	499	498	498	474	487
ψ_1^{AB}			-1	-1		—	-3	-2
ψ_1^{BA}								
ψ_2^{AB}			-1	-1	-1	-1	-3	-2
ψ_2^{BA}					1		1	1
S_1^A				1	1	1	-1	
S_1^B	1	1	2	2	2	2	9	7
S_2^A				1	1	1	-1	
S_2^B			2	2	2	2	9	7
constant	498	500	499	499	499	497	491	499
ψ^{AB}							-2	-1
ψ^{BA}								
S^A								
S^B			1	1	1	1	6	5

Note: Relative biases of capture probabilities and blank in the table are less than 1%.

TABLE 6. Relative standard errors (%) of estimates of p, ψ, S where either parameters vary over years or those are constant over years with low moving rate ($\psi = 0.25$), $p^A = p^B = 0.2$, $S^A = 0.7$, $S^B = 0.5$, $N = 1000$. There are three years of tag-recovery and two states

p, ψ, S variable	$\alpha = 4$ $\beta = 2$	$\alpha = 8$ $\beta = 3$	$\alpha = 1$ $\beta = 1$	$\alpha = 2$ $\beta = 2$	$\alpha = 5$ $\beta = 5$	$\alpha = 8$ $\beta = 8$	$\alpha = 2$ $\beta = 3$	$\alpha = 5$ $\beta = 7$
p_1^A	6.72	6.72	6.72	6.73	6.70	6.73	6.72	6.72
p_1^B	6.15	6.14	6.15	6.15	6.15	6.15	6.14	6.14
p_2^A	6.14	6.13	6.14	6.13	6.15	6.15	6.16	6.16
p_2^B	5.63	5.65	5.61	5.61	5.57	5.60	5.62	5.63
p_3^A	6.40	6.40	6.40	6.40	6.40	6.41	6.40	6.40
p_3^B	6.33	6.33	6.33	6.34	6.33	6.34	6.33	6.33
ψ_1^{AB}	16.52	16.52	17.04	17.09	17.22	17.24	17.75	17.65
ψ_1^{BA}	15.83	16.02	15.79	15.77	15.69	15.78	15.84	15.70
ψ_2^{AB}	14.57	14.32	15.57	15.61	15.61	15.60	16.37	16.25
ψ_2^{BA}	17.44	17.47	17.45	17.48	17.44	17.44	17.73	17.54
S_1^A	7.46	7.37	7.96	8.01	8.04	8.04	8.45	8.42
S_1^B	9.30	9.14	9.91	9.86	9.81	9.80	10.19	10.12
S_2^A	9.36	9.16	9.85	9.88	9.87	9.91	10.40	10.35
S_2^B	10.45	10.36	10.92	10.91	10.87	10.91	11.35	11.23
constant								
p^A	3.72	3.72	3.71	3.71	3.71	3.71	3.72	3.71
p^B	3.57	3.58	3.56	3.56	3.56	3.56	3.57	3.57
ψ^{AB}	9.77	9.57	10.38	10.41	10.38	10.43	10.94	10.78
ψ^{BA}	9.99	10.27	9.97	9.96	9.96	9.94	10.02	9.95
S^A	5.16	5.08	5.51	5.54	5.56	5.56	5.84	5.81
S^B	6.24	6.20	6.66	6.62	6.62	6.61	6.83	6.79

TABLE 7. Relative standard errors (%) of estimates of p, ψ, S where either parameters vary over years or those are constant over years with low moving rate ($\psi = 0.75$), $p^A = p^B = 0.2$, $S^A = 0.7$, $S^B = 0.5$, $N = 1000$. There are three years of tag-recovery and two states

p, ψ, S variable	$\alpha = 4$ $\beta = 2$	$\alpha = 8$ $\beta = 3$	$\alpha = 1$ $\beta = 1$	$\alpha = 2$ $\beta = 2$	$\alpha = 5$ $\beta = 5$	$\alpha = 8$ $\beta = 8$	$\alpha = 2$ $\beta = 3$	$\alpha = 5$ $\beta = 7$
p_1^A	6.73	6.72	6.73	6.72	6.71	6.73	6.64	6.64
p_1^B	6.13	6.15	6.16	6.15	6.14	6.14	6.11	6.10
p_2^A	5.96	5.92	6.04	6.06	6.05	6.05	5.92	5.98
p_2^B	5.63	5.66	5.59	5.58	5.57	5.58	5.59	5.49
p_3^A	6.41	6.39	6.40	6.38	6.40	6.40	6.37	6.34
p_3^B	6.31	6.33	6.25	6.24	6.24	6.25	6.13	6.19
ψ_1^{AB}	5.49	5.25	7.45	7.49	7.56	7.54	12.87	11.45
ψ_1^{BA}	5.98	5.88	7.94	7.86	7.79	7.78	11.60	10.65
ψ_2^{AB}	5.25	4.92	7.84	7.94	7.98	7.99	14.09	12.49
ψ_2^{BA}	6.01	5.78	7.93	7.84	7.78	7.76	11.86	10.75
S_1^A	11.20	9.78	19.40	19.62	19.90	19.94	32.57	29.78
S_1^B	12.23	10.87	22.10	21.84	21.75	21.69	37.81	34.66
S_2^A	13.10	11.65	21.70	22.02	22.24	22.33	34.63	32.00
S_2^B	14.23	12.50	25.33	25.21	25.14	25.06	40.75	37.78
constant								
p^A	3.64	3.65	3.64	3.64	3.64	3.63	3.62	3.63
p^B	3.58	3.58	3.56	3.57	3.57	3.56	3.58	3.56
ψ^{AB}	3.78	3.60	5.51	5.57	5.62	5.63	11.02	9.51
ψ^{BA}	4.11	4.00	5.55	5.48	5.42	5.42	9.66	8.47
S^A	8.69	7.49	15.66	15.97	16.22	16.32	29.32	26.18
S^B	9.38	8.29	17.55	17.35	17.19	17.18	24.47	30.24

there are fewer parameters to estimate. With low moving rate, $\psi = 0.25$, $\hat{\psi}$ usually has the highest RSE, and \hat{p} the lowest. However, with high moving rate, $\psi = 0.75$, \hat{S} usually has the highest RSE, and \hat{p} or $\hat{\psi}$ the lowest (Tables 6 and 7).

The precision of the estimates improves when there is a high capture rate ($p = 0.4$) versus a low capture rate ($p = 0.1$).

We have the correlations (Appendix B.19-27 of Joe & Pollock, 2001) to each case of $\alpha > \beta$, $\alpha = \beta$, or $\alpha < \beta$, for $\psi = 0.75$. \hat{S} and $\hat{\psi}$ for the same areas had progressively stronger negative correlation with a range of -0.46 to -0.14 when $\alpha > \beta$, -0.76 to -0.44 when $\alpha = \beta$, or -0.94 to -0.59 when $\alpha < \beta$. \hat{S} and $\hat{\psi}$ for the different areas had progressively stronger positive correlation with a range of 0.47 to 0.11 when $\alpha > \beta$, 0.79 to 0.44 when $\alpha = \beta$, or 0.92 to 0.60 when $\alpha < \beta$. The correlation of ψ s for different areas ($(\psi_1^{AB}, \psi_1^{BA}), (\psi_2^{AB}, \psi_2^{BA})$) was progressively more negative, with a range of -0.02 to -0.37 when $\alpha > \beta$, -0.66 to -0.38 when $\alpha = \beta$, or -0.90 to -0.53 when $\alpha < \beta$. The correlation of \hat{S} s for different areas ($(S_1^A, S_1^B), (S_2^A, S_2^B)$) was progressively more negative, with a range of -0.57 to -0.25 when $\alpha > \beta$, -0.86 to -0.65 when $\alpha = \beta$, or -0.93 to -0.75 when $\alpha < \beta$.

5 Numerical work on the capture-recapture model

We now present the results of a small simulation study with a uniform distribution for capture-recapture data carried out with the program SURVIV (White, 1983). We allowed the following factors to vary in $18 (= 3 \times 2 \times 3)$ cases, choosing values that we thought spanned a range of likely practical situations: (1) N , number tagged: we considered $N = 500$, $N = 1000$ or $N = 2000$ tagged in each period; (2) ψ , movement rate: we considered $\psi = 75\%$ (high) or $\psi = 25\%$ (low); (3) p , recovery rate: we kept p constant for each patch and each year, but assigned values: 0.1 , 0.2 , or 0.4 ; (4) S^A and S^B , survival rates: we kept these constant each year, but assigned these values: when $p = 0.1$, $S^A = 0.8$, $S^B = 0.6$; when $p = 0.2$, $S^A = 0.7$, $S^B = 0.5$; when $p = 0.4$, $S^A = 0.6$, $S^B = 0.4$.

We carried out 500 simulations for each run (18 cases). We considered the relative bias of the estimates and the relative standard errors of the estimates as in the last section.

We found the bias to be very small ($< 2\%$ of the true parameters in most cases) for the simulations. For the simulations with $p = 0.1$, $S^A = 0.8$, $S^B = 0.6$, the bias was greatest for \hat{S} ($< 14\%$ when $N = 500$, $< 11\%$ when $N = 1000$ and $< 7\%$ when $N = 2000$). When S was held constant over the years (the reduced model), the bias effectively halved.

The RSEs are smaller when more animals are tagged. The RSEs are much smaller when ψ , S can be assumed to be constant over the years because then there are fewer parameters to estimate. With low moving rate, $\psi = 0.25$, $\hat{\psi}$ usually has the highest and \hat{S} the lowest RSE. However, with high moving rate, $\psi = 0.75$, \hat{S} usually has the highest and $\hat{\psi}$ the lowest RSE. The precision of the estimates improves when there is a high capture rate ($p = 0.4$) versus a low capture rate ($p = 0.1$).

For $\psi = 0.75$, \hat{S} and $\hat{\psi}$ for the same areas had a substantial negative correlation with a range of -0.81 to -0.43 ($(\psi_i^{AB}, S_i^B), (\psi_i^{BA}, S_i^A)$), \hat{S} and $\hat{\psi}$ for the different areas had a substantial positive correlation, with a range of 0.83 to 0.46 ($(\psi_i^{AB}, S_i^A), (\psi_i^{BA}, S_i^B)$). The correlation of ψ s for different areas ($(\psi_i^{AB}, \psi_i^{BA})$) was substantially negative, with a range of -0.85 to -0.51 . The correlation of \hat{S} for different areas ((S_i^A, S_i^B)) was strongly negative, with a range of -0.89 to -0.70 (see also Appendix B.28-30 of Joe & Pollock, 2001).

6 An example

Iwao (1963) developed a simple model for estimating the rate of population interchange between two areas, showing an example with the movement between two different food plants by an adult population of insects (*Epilachna vigintioctomaculata*).

Arnason (1972) developed the model further with losses due to emigration or death occurring, but not gains due to recruitment or immigration, in order to estimate population size, transition and capture probabilities. He used moment equations, not MLEs. He modified the data reported by Iwao (1963) to illustrate his model. He also developed another example for much the same amount of sampling effort. He did simulations based on the modified data using the estimates, as though they were true parameters.

We attempted to analyse the insect data of Iwao (1963) but supplemented in the way described by Arnason (1972) as a special case of our model. We had to use the constraint of constant capture probabilities in each area ($p_2^A = p_3^A$; $p_2^B = p_3^B$) to achieve convergence. We also did simulations based on the separation of survival and movement rates with both losses (emigration or death) and gains (immigration or birth). We used the method derived earlier in this chapter, and obtained MLEs.

In Table 8, we compare Arnason’s and our models on the results of the simulation experiment. The true values of the parameters, used to generate the data on the computer, are given in the first column. Given these values, the expected values of the caught and marked animal numbers, such as (N_i^r, R_{ij}^{rs}) in our model, can be calculated. Values of the parameters were selected such that these expected values were close to the actual observations reported by Iwao (1963). The experiment was simulated 1000 times and, at the end of each simulation, the parameter estimates were calculated. At the end of the experiment, the mean and variance for each estimate was calculated. In Table 8, capture probability and transition probability estimates (standard errors) are given.

The precision and bias of some of our estimates are much better, although those of some of the estimates are the same.

We also computed survival and movement rates separately, which was not done in Arnason (1972), assuming movement occurs randomly with a uniform distribution (Table 9). The movement rates are moderate (i.e. around 30%) in all cases.

TABLE 8. The estimates for Iwao insect data

	True parameter	Arnason’s	Joe & Pollock’s
p_2^A	0.35	0.418 (0.795)	0.428 (0.229)
p_2^B	0.60	0.670 (1.222)	0.611 (0.103)
p_3^A	0.30		0.428 (0.229)
p_3^B	0.60		0.611 (0.103)
ϕ_1^{AA}	0.35	0.387 (0.458)	0.345 (0.155)
ϕ_1^{AB}	0.20	0.187 (0.234)	0.198 (0.065)
ϕ_1^{BA}	0.15	0.166 (0.322)	0.160 (0.094)
ϕ_1^{BB}	0.55	0.544 (0.172)	0.546 (0.083)
$\phi_2^{AA} p_3^A$	$(0.35)(0.30) = 0.105$	0.106 (0.033)	0.106 (0.032)
$\phi_2^{AB} p_3^B$	$(0.20)(0.60) = 0.12$	0.117 (0.034)	0.117 (0.035)
$\phi_2^{BA} p_3^A$	$(0.15)(0.30) = 0.045$	0.045 (0.013)	0.045 (0.013)
$\phi_2^{BB} p_3^B$	$(0.55)(0.60) = 0.33$	0.329 (0.029)	0.328 (0.029)

TABLE 9. The Iwao estimates with separation of survival and movement rates

	Parameter	Mean (s.d.)
	p_2^A	0.35 0.428 (0.229)
	p_2^B	0.60 0.611 (0.103)
	p_3^A	0.30 0.428 (0.229)
	p_3^B	0.60 0.611 (0.103)
	ψ_1^{AB}	0.32 0.339 (0.135)
	ψ_1^{BA}	0.25 0.252 (0.118)
	ψ_2^{AB}	0.32 0.353 (0.126)
	ψ_2^{BA}	0.25 0.227 (0.098)
	S_1^A	0.51 0.505 (0.161)
	S_1^B	0.73 0.738 (0.093)
	S_2^A	0.51 0.457 (0.173)
	S_2^B	0.73 0.715 (0.108)

With \hat{S} and $\hat{\psi}$ for the same areas, we found (ψ_i^{AB}, S_i^B) and (ψ_i^{BA}, S_i^A) had a moderately positive correlation with a range of 0.56 to 0.39. (ψ_i^{AB}, S_i^A) and (ψ_i^{BA}, S_i^B) had a negative correlation, with a range of -0.53 to -0.37 , exploring \hat{S} and $\hat{\psi}$ for the different areas. The correlation of ψ s for different areas $((\psi_i^{AB}, \psi_i^{BA}))$ was negative, with a range of -0.57 to -0.37 .

7 Discussion

The recent interest of ecologists and conservation biologists in landscape ecology, fragmentation and meta-population dynamics has focused their attention on patch survival rates and between-patch movement rates. For the models described in this chapter, the decomposition of transition probabilities into survival and movement probabilities provides the appropriate framework for estimating parameters of interest.

For a known distribution for movement time, t , the uniform distribution case is important as it corresponds to random movement. The case in which movement time is a random variable with the beta distribution requires good estimates of α and β . These could come from biological knowledge or from putting radio tags on the animals. Powell *et al.* (2000) has used radio-telemetry data and capture-recapture data to study movement, but used a different model from our model.

Radio-telemetry has been used extensively to study animal movement in recent years. It would be possible to use capture-recapture or tag-return methods together with radio-telemetry to study movements within a meta-population system. For the models described here, the decomposition of transition probabilities into survival and movement probabilities requires a specific ordering of conditional events (Fig. 1). We have assumed that the conditional movement rate does not depend on the movement time. Additional data from telemetry animals could be used to test this assumption. More importantly, such data could be used to relax the assumption by permitting estimation of one survival probability for animals that remain in a patch and another for animals that leave the patch. Of course, one could also use the telemetry data to get an estimate of $f(t)$, the probability density function for movement time as in Powell *et al.* (2000). As we discussed earlier in this paper, we did not consider the robustness of our inference to misspecification of the random movement distribution ($f(t)$). We plan on including this aspect in future work.

There also needs to be more work on other assumptions, such as equal catchability. There could also be work on population size estimation.

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